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TAXONOMIC ASSESSMENT OF THE
CTENOPHORUS DECRESII COMPLEX (REPTILIA: AGAMIDAE)
REVEALS A NEW SPECIES OF DRAGON LIZARD
FROM WESTERN NEW SOUTH WALES

by

CLAIRE A. McLEAN,
ADNAN MOUSSALLI, STEVE SASS, & DEVI STUART-FOX

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Taxonomic Assessment of the *Ctenophorus decresii* Complex (Reptilia: Agamidae) Reveals a New Species of Dragon Lizard from Western New South Wales

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ABSTRACT. We describe a new species of agamid lizard, *Ctenophorus mirrityana* sp.nov. currently known from two disjunct populations in western New South Wales. The species is a member of the *C. decresii* species complex, and was formerly recognized as an outlying population of *C. decresii* due to similarities in dorsal colour pattern and adjacent distributions. Previous work documented deep molecular divergence, across multiple loci, with no genetic admixture between the new species and proximal *C. decresii* populations. We find that the new species differs in morphology from all other members of the species complex and is characterized by distinct male throat and lateral coloration, a small head size relative to snout-vent length, a large number of labial scales, and a lack of tubercular scales. We also identify two geographically structured lineages (*northern* and *southern*) within *C. decresii* as requiring further taxonomic investigation, based on notable genetic and morphological (including colour) divergence. We find that divergence in coloration is associated with genetic and body form differentiation within the *C. decresii* species complex.

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KEYWORDS: Agamidae; Barrier Range; colour variation; *Ctenophorus mirrityana*; reptilian morphology

Ctenophorus is the most diverse Australian genus of agamid lizards, comprising 28 small to moderate sized, dry to arid adapted species (Houston & Hutchinson, 1998; Wilson & Swan, 2010). Within South Australia (SA), the *Ctenophorus decresii* complex consists of four closely related, rock-inhabiting species: *C. decresii* (Duméril & Bibron 1837),

C. fionni (Procter 1923), *C. tjantjalka* Johnston 1992, and *C. vadrappa* (Houston 1974), with *C. rufescens* (Stirling & Zietz 1893) as a sister clade to the group (Melville *et al.*, 2001; Chen *et al.*, 2012). All species are sexually dimorphic with cryptically coloured females and larger, brightly coloured males which perform conspicuous courtship and

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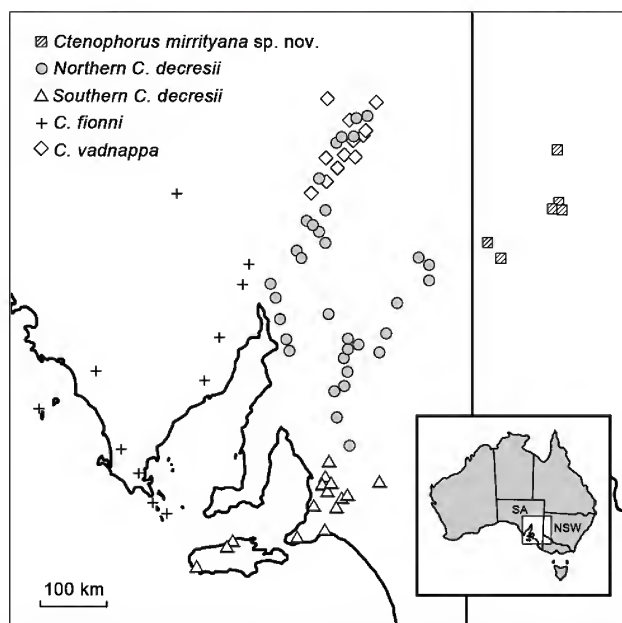


Fig. 1. Map showing sampling localities of material examined in this study, incorporating the full distributions of *Ctenophorus mirrityana* sp. nov., northern *C. decresii*, and southern *C. decresii*.

territorial behaviour (Gibbons, 1979). Overall body form is highly conserved within the group and reflects adaptation to rocky habitats; all species have dorsoventrally flattened heads and bodies (less so in *C. tjantjalka*) and long hindlimbs (Houston & Hutchinson, 1998). While females and juveniles are similar in appearance among species, male coloration is an obvious distinguishing feature between species (Houston, 1974), and is likely to be an important social signal within the *C. decresii* complex (Osborne, 2005; Stuart-Fox & Johnston, 2005).

The tawny dragon, *Ctenophorus decresii*, exhibits remarkable variation in coloration both within and among populations (Houston, 1974; Teasdale *et al.*, 2013; McLean *et al.*, submitted). The species inhabits rocky areas throughout the Flinders, Olary, and Mt Lofty Ranges, and on Kangaroo Island in SA. Peripheral isolated populations occur in the Barrier Range, western New South Wales (NSW, Fig. 1). A recent phylogeographic study revealed three genetic lineages within *C. decresii*, each corresponding with distinct male throat coloration (McLean *et al.*, submitted; Fig. 2). Two lineages occur in South Australia (SA) forming a *northern* and *southern* lineage (Fig. 1) consistent with the two “races” delineated by Houston (1974). The *northern* lineage is polymorphic, exhibiting four discrete male throat colour morphs within populations: orange, yellow, orange and yellow, and grey (Teasdale *et al.*, 2013; Fig. 3), which is fixed at sexual maturity (Osborne, 2004; Stuart-Fox, unpublished data). Conversely, the *southern* lineage is monomorphic; all males have blue throats with yellow to orange coloration along the gular fold (McLean *et al.*, submitted; Fig. 3). Secondary contact between the *northern* and *southern* lineage was found centred on the Barossa Valley, SA. While limited genetic introgression was evident at the contact zone, no phenotypic intermediates were found, suggesting that potential pre- or post-zygotic barriers to gene flow may exist between the *northern* and *southern* lineages (McLean *et al.*, submitted).

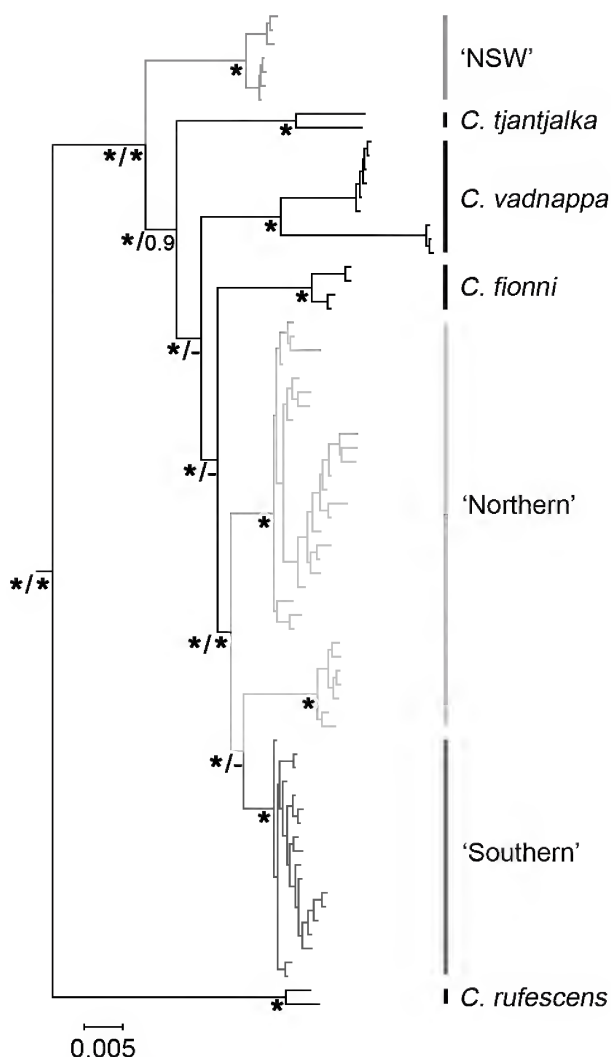


Fig. 2. Combined mtDNA (ND4) and nuDNA (α -enolase, BACH1, FSHR, MKL1, SLC8A1) sequence data tree, rooted with *C. pictus* (not shown). Grey branches represent *C. decresii* lineages. Asterisks indicate posterior probabilities > 0.95 generated from MrBayes and *BEAST analyses respectively, unless otherwise indicated.

The third lineage, representing the isolated NSW populations, is further distinguishable by unique throat coloration; males have cream throats with a black central stripe and orange flushes (Fig. 3). The “NSW lineage” exhibited substantial molecular differentiation with 7.1–9.6% corrected mtDNA (ND4) net sequence divergence between NSW and SA populations (McLean *et al.*, submitted). Furthermore, the multi-locus phylogenetic analyses strongly indicated polyphyly of *C. decresii*, with the NSW lineage being basal and sister to all other members of the species group (McLean *et al.*, submitted; Fig. 2). Applying a conservative mitochondrial calibration of 2% sequence divergence per million years, this level of divergence suggests separation during the Pliocene, approximately 5–3.5 Mya, a period of cladogenesis broadly consistent with that for *C. fionni*, *C. tjantjalka*, and *C. vadrappa* (7–4.8 Mya; Melville *et al.*, 2001; Hugall *et al.*, 2008; Chen *et al.*, 2012).

Table 1. Morphometric measurements and meristic counts used in this study.

abbreviation	definition of character
SVL	Snout-vent length
TL	Tail length (unbroken tails only)
AG	Axilla-groin length
HL	Head length, from tip of snout to posterior of jaw bone
HW	Head width at widest point
HD	Head depth at deepest point
EYE	Eye diameter
SL	Snout length from tip of snout to anterior of eye
JL	Jaw length from posterior of eye to posterior of jaw bone
NW	Width between nostrils
HUML	Humerus length
RADL	Radius length
HAND	Hand length from wrist to tip of fourth finger
FING	Fourth finger length
FEML	Femur length
TIBL	Tibia length
FOOT	Foot length from ankle to tip of fourth toe
TOE	Fourth toe length
SUPRA	Number of supralabial scales
INFRA	Number of infralabial scales
ROSNAS	Number of scales between rostral and nasal
SUPRNAS	Number of scales between supralabial and nasal
INTERNAS	Number of internasal scales across the top of the snout
SDL	Number of subdigital lamellae
FP	Number of femoral pores (males only)

Here we present a taxonomic revision of *C. decresii* sensu lato and conduct a detailed morphological assessment in light of the phylogenetic hypothesis arising from consideration of the molecular data. Based on significant genetic, colour, and body form divergence, we describe a new member of the *C. decresii* species complex from western NSW. We also recognize the northern and southern lineages of *C. decresii* as potentially warranting sub-specific status based on phenotypic divergence between the two lineages and a lack of phenotypic admixture at the contact zone. However, further work characterising clines in phenotypic and genetic markers across the contact zone is needed to resolve the taxonomic and conservation status of these two SA lineages.

Materials and methods

Morphological analysis was based on morphometric measurements and meristic counts of preserved material held in the Australian Museum, Sydney (AMS), South Australian Museum (SAM), and Museum Victoria (NMV). Morphological character definitions and abbreviations are listed in Table 1. All measurements were made with digital callipers to the nearest 0.1 mm, with the exception of tail length (TL) which was to the nearest 0.5 mm (unbroken tails only). We examined all available adult specimens of the new taxon (N = 51) along with a representative sample of *northern* (N = 70) and *southern* (N = 40) *C. decresii*, and a small number of *C. fionni* (N = 15) and *C. vadrappa* (N = 15) for interspecific comparison (Appendix 1; Fig. 1). Specimens with SVL ≥ 65 mm for males and ≥ 60 mm for females were considered to be adults. For analysis, all morphometric measurements were adjusted relative to snout-vent length (SVL) by taking the ratio of each

measurement to SVL. In addition, males and females were analysed separately to account for sexual dimorphism. After confirming that there were no strong correlations between variables (PROC CORR; SAS 9.3), we assessed whether individuals clustered into the five species/lineages based on morphology using a discriminant function analysis (DFA; PROC DISCRIM; SAS 9.3). All measurements and meristic counts were included as response variables in the analysis, with the exception of TL, which was excluded due to the large number of individuals with broken tails (in total, 24 variables for males and 23 variables for females; Table 1). We performed Tukey's *post hoc* tests and employed false discovery rate (FDR) correction for multiple tests (PROC MULTTEST; SAS 9.3) to determine which variables differed significantly among taxa.

Results

Discrimination of the five taxa (*Ctenophorus mirrityana* sp. nov., *northern C. decresii*, *southern C. decresii*, *C. fionni*, and *C. vadrappa*) was highly significant (males: Wilks' $\lambda = 0.027$, $F_{96,296} = 4.16$, $P < 0.0001$; females: Wilks' $\lambda = 0.049$, $F_{92,232} = 2.89$, $P < 0.0001$), and a combination of canonical variables 1 (*can 1*) and 2 (*can 2*) explained 82.07% and 86.20% of the variation for males and females respectively (Table 2). The overall correct assignment rate for males was 70%, with 94.4% of *C. mirrityana* sp. nov., 90.5% of *southern C. decresii*, 53.5% of *northern C. decresii*, 50% of *C. fionni*, and 60% of *C. vadrappa* specimens assigned correctly. Notably, 23.3% of *northern C. decresii* specimens were incorrectly grouped with *C. fionni*, while only 4.6% were grouped with *southern C. decresii*. Correct identification rate was lower for females than for males (50% overall) with 74.2%

Table 2. Standardized canonical discriminant function coefficients for the first two canonical variables for males and females. Characters strongly correlated with canonical variables (large absolute values) are bold and italicized.

variable	male		female	
	canonical 1	canonical 2	canonical 1	canonical 2
SVL	-0.689	0.844	0.502	0.445
AG/SVL	-0.147	0.237	-0.112	-0.053
HL/SVL	0.683	-0.454	0.035	-0.167
HW/SVL	-0.072	0.349	0.293	-0.269
HD/SVL	0.429	0.280	-0.631	0.531
EYE/SVL	0.047	0.226	0.161	0.015
SL/SVL	0.012	0.096	-0.471	0.070
JL/SVL	-0.405	0.823	-0.093	0.081
NW/SVL	0.169	0.363	-0.153	0.352
HUML/SVL	0.164	-0.014	-0.504	0.465
RADL/SVL	0.612	0.203	-0.063	-0.719
HAND/SVL	-0.646	0.346	-0.498	0.275
FING/SVL	0.349	-0.229	0.621	0.215
FEML/SVL	-0.239	0.341	0.457	0.896
TIBL/SVL	-0.828	0.227	0.711	-1.030
FOOT/SVL	-0.147	0.129	0.393	0.249
TOE/SVL	0.091	-0.082	0.146	-0.214
SUPRA	-0.279	-0.255	-0.448	0.625
INFRA	-0.902	0.192	0.911	0.552
ROSNAS	0.119	0.125	0.155	-0.411
SUPRANAS	-0.071	0.185	0.411	-0.878
INTERNAS	0.548	0.181	-0.823	0.430
SDL	0.145	-0.162	-0.545	0.085
FP	0.758	-0.251		
F-value	4.61	2.81	2.89	1.64
p-value	<0.0001	<0.0001	<0.0001	0.006
Eigenvalue	4.843	1.330	3.937	1.116
Proportion of Variance	0.644	0.177	0.672	0.190

C. mirrityana sp. nov., 31.6% *southern C. decresii*, 64% *northern C. decresii*, 60% *C. fionni*, and 20% *C. vadrappa* classified into correct groups, thus reinforcing the similarity of females among species within the complex. Overall, the correct identification rate was higher for *C. mirrityana* sp. nov. than for all other taxa.

For males, *can 1* most clearly separated *Ctenophorus mirrityana* sp. nov. from all other taxa, followed by separation of *northern* and *southern C. decresii*, with the number of infralabial scales, tibia length, number of femoral pores, snout-vent length, and size-corrected head length contributing most strongly to the discriminant function (Table 2). *Can 2* most clearly separated *C. vadrappa* from *C. mirrityana* sp. nov. and *southern C. decresii*, with the strongest contributing variables being snout-vent length and size-corrected jaw length (Table 2). Discrimination was less pronounced in females than in males, and the low sample sizes ($N = 5$) for *C. fionni* and *C. vadrappa* resulted in considerable overlap in 95% confidence ellipses (Fig. 4B). For females, *can 1* distinguished *C. mirrityana* sp. nov. from *northern* and *southern C. decresii*, with the number of infralabial scales, number of internasal scales, and size-corrected tibia length contributing most strongly to the discriminant function (Table 2). Size-corrected tibia

length, femur length, and radius length, and the number of scales between supralabial and nasal contributed strongly to *can 2* (Table 2).

Univariate analyses for males and females were largely consistent with the discriminant function analysis (DFA, see Appendix 2). In addition to the variables contributing strongly to the DFA, significant differences were found for ten and three other characters for males and females respectively. These additional characters primarily reflected moderate correlations among some of the morphological characters examined (see Appendix 3). Based on Tukey's *post-hoc* tests, *C. mirrityana* sp. nov. males have significantly smaller head measurements (HL, HW, HD, SL, JL, and NW), and a greater number of supralabial and infralabial scales than all other taxa (Fig. 5). Similarly, head length and snout length of *C. mirrityana* sp. nov. females were generally smaller than in other taxa (Fig. 6). *Ctenophorus mirrityana* sp. nov. is further distinguished from *C. decresii* in having fewer internasal scales in both males and females, fewer femoral pores in males, and longer hindlimbs (FEML, TIBL) in females (Fig. 5, 6).

Within *C. decresii* notable morphological separation was observed between the *northern* and *southern* lineage (Fig. 4). *Southern C. decresii* (both males and females) are smaller (SVL) than *northern C. decresii* and have fewer supralabial and infralabial scales (Fig. 5, 6). Furthermore, *southern* males have a greater number of femoral pores, shallower heads (HD), and shorter jaws (JL) than *northern* males (Fig. 5).

Taxonomy

Ctenophorus mirrityana sp. nov.

Barrier Range Dragon

Figs 3A, 7, 8, 9A

Holotype. AMS R47295 (Fig. 8), an adult male with label data: Australia, New South Wales, Mootwingee [Historic Site, Mutawintji National Park], 31°17'S 142°18'E, 20 January 1975, collector P. Rankin *et al.* [Office of Environment and Heritage].

Paratypes. All specimens are from New South Wales. AMS R14661, Mootwingee Waterholes (31°19'S 142°19'E); AMS R45527–9, AMS R47294, AMS R47298, AMS R47335, AMS R61514, AMS R68792, AMS R125297, AMS R133122–3, AMS R145339, AMS R145341, AMS R145593, AMS R146252–3, AMS R149014, AMS R149021, AMS R149143, AMS R149146–7, AMS R151011–2, AMS R151014–7, AMS R151019–20, AMS R151733–5, AMS R153361, AMS R154857, AMS R154859, AMS R154863–4, AMS R154869–70, AMS R154872, AMS R154932–8, AMS R157300–7, AMS R157317–23, AMS R157325–8, AMS R157330–40, AMS R157342, AMS R157344, AMS R157346–9, SAM R5194A–B, SAM R14468A–B, SAM R31655, NMV D11511, NMV D11770, NMV D18019, NMV D40134–5, NMV D50516, NMV D56318–22, Mootwingee National Park (31°17'S 142°18'E), AMS R107358–67, 6 km S Mootwingee National Park (31°18'S 142°15'E), AMS R161707–8, Homestead Gorge, Mootwingee National Park (31°16'35"S 142°18'5"E), NMV D56323, Broken Hill (31°58'S 141°27'E), AMS R50540, Koonenberry Mountain (30°31'S 142°18'E), AMS R168437, "Belmont Station", N Silvertown (31°46'11"S 141°14'33"E).

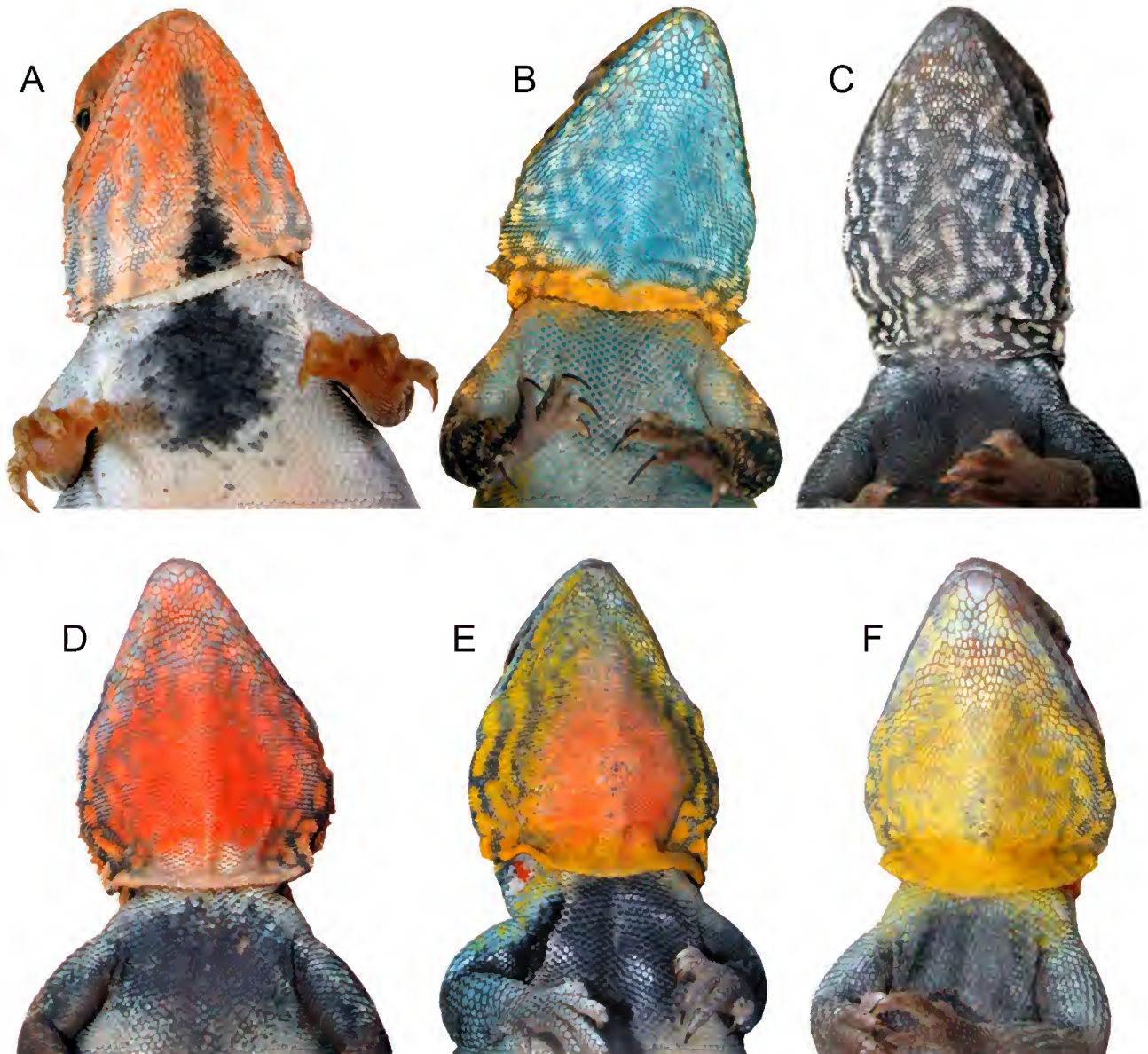


Fig. 3. Male throat coloration of *Ctenophorus mirrityana* sp. nov. (A), southern *C. decresii* (B), and the four colour morphs of northern *C. decresii*: grey (C), orange (D), orange and yellow (E), and yellow (F) (photo C. McLean).

Diagnosis

A member of the *Ctenophorus decresii* species complex (Houston & Hutchinson, 1998), *C. mirrityana* sp. nov. is a moderately sized, sexually dimorphic, rock-dwelling dragon lizard with a strongly compressed head and body (Fig. 7). Within the species complex, *C. mirrityana* sp. nov. is distinguishable by the following combination of characters: head relatively small for body size; snout scales keeled or weakly wrinkled; vertebral scales flat and pale in colour; black lateral stripe from tympanum to groin; thinner, non-continuous orange stripe within black lateral stripe; flanks lack tubercular scales; male throat coloration pale cream with parallel grey stripes and black central stripe sometimes overlain with orange flushes.

Description

A moderately sized dragon lizard reaching a maximum SVL of approximately 91 mm and total length of 266 mm. Head strongly compressed and small for body size (relative to other members of the species complex; Appendix 2); nostril located beneath a sharp canthus rostralis. Body and base of tail dorsoventrally flattened, allowing the species to squeeze into narrow rock crevices. Tail long and evenly tapered to a fine tip; forelimbs moderately long reaching or almost reaching groin when adpressed; hindlimbs long and reaching or almost reaching snout when adpressed, digits are long and slender; finger lengths: $4 > 3 > 5 > 2 > 1$; toe lengths: $4 > 3 \geq 5 > 2 > 1$.

Characteristic of the genus *Ctenophorus*, a row of

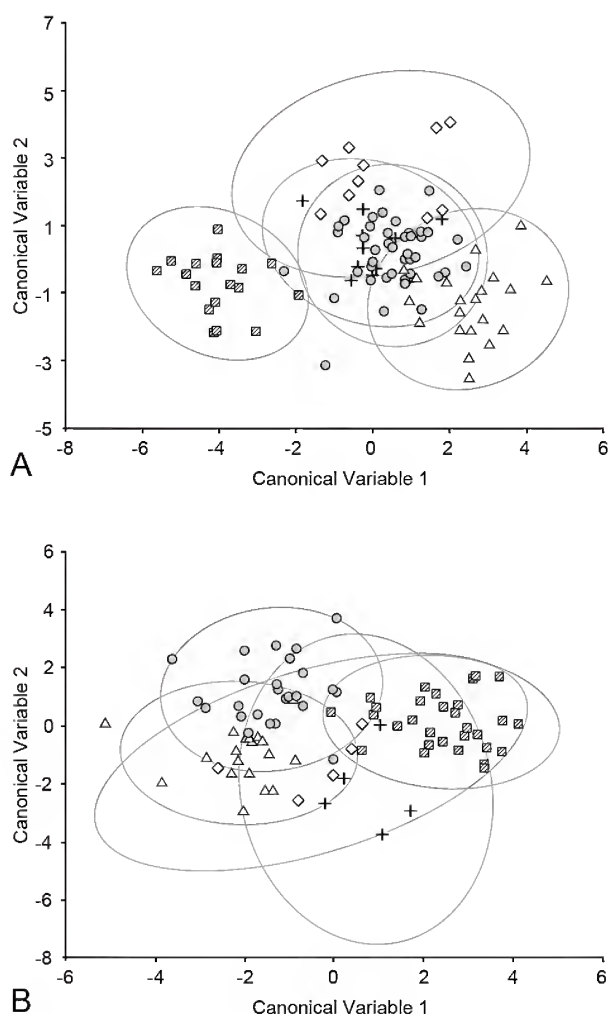


Fig. 4. Discriminant function analyses of male (A) and female (B) *Ctenophorus mirrityana* sp. nov. (■); northern *C. decresii* (○); southern *C. decresii* (△); *C. fionni* (+); and *C. vadrappa* (◇); based on 24 and 23 morphological characters respectively. Individuals are plotted against canonical variables 1 and 2 with 95% confidence ellipses.

enlarged, keeled scales extends from the nostril, below the eye to above the tympanum (Houston & Hutchinson, 1998). Scales on snout are keeled to lightly wrinkled; eyelid fringed with row of acute scales; 14–19 supralabial and infralabial scales; 4–6 scales between rostral and nasal; 4–6 scales between supralabial and nasal; 9–12 internasal scales; 21–27 subdigital lamellae on the fourth toe. The skin on the neck is loose, forming folds of skin above and behind the tympanum with small rows of pale coloured spines. A low nuchal crest of conical scales is present and terminates in line with the shoulders. Vertebral scales are flat and pale in colour and can be raised on a fold of skin during behavioural displays. Dorsal scales are smooth or very lightly keeled, becoming smaller laterally; flanks lack scattered tubercular scales. Scales on the dorsal surfaces of the limbs and tail are keeled. A strongly formed gular fold is present, extending across the shoulders. Ventral scales are around the same size as vertebral scales, larger than dorsal and lateral scales, flat and homogenous, with the exception of the scales along the gular fold which are smaller. Thirty four to forty two evenly spaced femoral and preanal pores are arranged in a straight

line along the thighs, interrupted medially by 7–9 scales. Pores are present but smaller in females.

Adult male base colour varies from grey-blue to very pale blue which appears more blue when the lizard is warm (Fig. 7A). The vertebral line is pale, becoming more grey-blue towards the flanks, while the dorsal surfaces of the head, tail and hindlimbs are grey-brown. The head is orange around the eyes, nostrils and along the upper jaw, and beneath the tympanum to the neck; however, the extent and brightness of this coloration varies among individuals. A black lateral stripe begins posterior to the eye, becoming thicker posterior to the tympanum and terminating at the groin. A thinner, non-continuous orange stripe, often bordered by pale blotches, begins at the tympanum and runs within the black lateral stripe to the groin (Fig. 9A). Pale blue coloration mottled with cream occurs beneath the lateral stripe and on the forelimbs. Ventrally males are white to cream with orange flushes on the belly, hindlimbs, and tail during the breeding season. A grey to black chest patch tapers to a point midbody and extends along the forelimbs in some individuals. Male throat coloration consists of cream base colour with parallel grey stripes along the length of the throat, often overlain with orange flushes around the snout, which may cover the whole throat in some individuals (Fig. 3). A distinct black stripe runs along the mid line from gular fold to snout but varies in length and intensity among individuals.

Adult females are cryptically coloured with brown, grey, and terracotta speckling (Fig. 7B). Dorsally, scales are browner with a thin, pale vertebral line. A black lateral stripe coupled with a thin terracotta stripe runs laterally along the flank, although this may be less prominent than in males. Scales are greyer on the flanks below the lateral stripe. Ventrally females are white to cream with grey stripes on the throat and orange flushes on the belly during the breeding season. Juveniles resemble adult females in coloration and pattern but are often paler with more delicate speckling. Pattern remains clear on spirit preserved specimens; however, both males and females appear darker than in life and any orange coloration fades considerably.

Measurements (mm) and meristic counts of holotype.

SVL, 76.87; AG, 32.99; TL, 142; HL, 25.38; HW, 17.60; HD, 10.96; EYE, 5.47; SL, 8.31; JL, 13.07; NW, 6.79; HUML, 11.48; RADL, 9.46; HAND, 13.46; FING, 8.31; FEML, 18.72; TIBL, 20.89; FOOT, 27.52; TOE, 14.14; SUPRA, 17; INFRA, 17; ROSNAS, 4; SUPRANAS, 5; INTERNAS, 10; SDL, 21; FP, 36.

Ecology and distribution

Ctenophorus mirrityana sp. nov. is a rock specialist, and occupies variable habitats ranging from scattered rock aggregates and road spoils, to rocky outcrops and gorges (Swan & Foster, 2005; Sass & Swan, 2010). Previous studies associated with this species have suggested that the percentage cover of exposed rock outcropping, the presence of large rocks, and landscape position are the greatest influence of habitat occupancy (Sass & Swan, submitted). To date, *C. mirrityana* sp. nov. has been detected in mulga shrubland dominated by Mulga (*Acacia aneura*) and Dead Finish (*A. tetragonophylla*), black oak woodland dominated by Black Oak (*Casuarina pauper*) and Western Rosewood (*Alectryon oleifolius*), and hummock grass woodland dominated by Gum Coolibah (*Eucalyptus intertexta*) and Red Mallee (*E. socialis*)

with an understorey of Porcupine Grass (*Triodia scariosa* subsp. *scariosa*; Swan & Foster, 2005; Sass & Swan, 2010).

The species is active and conspicuous during hot weather and shelters in rock crevices when threatened or inactive. Males perform conspicuous courtship and territorial behaviour involving push-ups and tail-flicks, and will often perch in prominent positions during displays. *Ctenophorus mirrityana* sp. nov. is allopatric to all other members of the species group, and is currently known from four localities in western NSW. It has recently been recorded from Mutawintji National Park and adjacent properties (Swan & Foster, 2005), and the Silverton Wind Farm site, 35 km north west of Broken Hill (Sass & Swan, 2010). Additionally, museum specimens from Broken Hill and Koonenberry Mountain, north of Mutawintji National Park were collected in the 1970s (Fig. 1).

Etymology. The specific epithet *mirrityana* is a word meaning “out in the sunlight” in the local Aboriginal language (Paakantyi; Hercus, 1993), in reference to the conspicuousness of the species during hot weather. There are several rock engravings depicting lizards at Mutawintji National Park (McCarthy & Macintosh, 1962), some of which may represent this species given its prominence in the area. We propose Barrier Range Dragon as the species’ common name.

Comparison between species

Ctenophorus mirrityana sp. nov. strongly resembles *C. decresii* in coloration. In both species, male dorsal coloration consists of blue-grey base colour with a black lateral stripe and bright yellow-orange coloration around the head, however, throat coloration differentiates these species. The throat colour of *C. mirrityana* sp. nov. is cream with grey stripes, overlain with orange flushes, with a black central stripe. The black stripe is distinct to the species, although some *northern C. decresii* individuals may have a small, central black patch on their throat. Conversely, *northern C. decresii* males have orange, yellow, orange and yellow, or grey throats (Teasdale *et al.*, 2013) and *southern C. decresii* males have blue or blue and yellow throats (Houston, 1974). Differences in lateral colour pattern further distinguish *C. mirrityana* sp. nov. and *C. decresii* (Fig. 9). *Ctenophorus mirrityana* sp. nov., has a non-continuous stripe of orange coloration which runs within a black lateral stripe between the tympanum and groin (Fig. 9A). In *southern C. decresii*, the lateral stripe is “pinched” along its length by the margining yellow-orange coloration and is interrupted on the neck, forming a separate black blotch behind the tympanum (Fig. 9B). Conversely, the black lateral stripe of *northern C. decresii* is relatively straight edged and continuous, and a cream, yellow or orange stripe runs along its upper edge and generally terminates just posterior to the shoulder (Fig. 9C). In other aspects of morphology, the head of *C. mirrityana* sp. nov. is smaller (relative to SVL) than that of *C. decresii*, and *C. mirrityana* sp. nov. has fewer internasal scales, fewer femoral pores, a greater number of supralabial and infralabial scales, a prominent pale vertebral line, and lacks scattered white tubercular scales on the flanks.

Notable phenotypic differentiation exists between *C. mirrityana* sp. nov. and the other members of the *C. decresii* species group. *Ctenophorus mirrityana* sp. nov. has a blue-grey body colour with a black lateral stripe compared with vertical orange-red and black flank markings in *C. vadrappa*, rows of pale spots in *C. fionni*, and a grey-brown body colour with pale lateral blotches forming vertical bars

in *C. tjantjalka*. Male *C. mirrityana* sp. nov. have cream throat coloration with grey stripes, a black central stripe, and orange flushes compared with yellow and blue in *C. vadrappa*, cream and yellow in *C. fionni*, and cream with fine grey reticulations in *C. tjantjalka*. Furthermore, while *C. mirrityana* sp. nov. has a dorsoventrally flattened head and smooth or weakly keeled snout scales, *C. tjantjalka* has a relatively short and deep head and coarsely wrinkled snout scales (Johnston, 1992). Snout scales are similarly wrinkled in *C. vadrappa* (Houston, 1974), which also has longer hindlimbs than *C. mirrityana* sp. nov. (Fig. 5). The distribution of *C. mirrityana* sp. nov. does not overlap with any other member of the group (Fig. 1); however, it may be about the most eastern populations of *northern C. decresii* around the SA/NSW border. Consequently, *C. mirrityana* sp. nov. is most likely to be confused with *northern C. decresii* based on distribution.

The *northern* and *southern* lineages of *C. decresii* are further distinguishable from each other by coloration (as described above) and a combination of other morphological characters. *Southern C. decresii* is generally smaller, has fewer supralabial and infralabial scales, and a greater number of femoral pores than *northern C. decresii*. Furthermore, *southern C. decresii* individuals consistently have prominent white tubercular scales along their flanks, which are often absent in *northern* individuals.

Conservation status

The distribution of *C. mirrityana* sp. nov. is sufficiently restricted that it was (as *C. decresii*) formerly recognized as endangered in NSW (NSW Scientific Committee, 2002). The species distribution currently exists as two disjunct populations approximately 100 km apart; however, no field surveys have been undertaken in the intervening areas and *C. mirrityana* sp. nov. may be more widespread throughout the Barrier Range region than currently appreciated. Alternatively, these populations may be relicts of a previously wider distribution and under this scenario *C. mirrityana* sp. nov. may warrant Federal nomination as a threatened species under the Environmental Protection and Biodiversity Conservation Act (1999). Field surveys of other suitable sites are needed to determine the full distribution of the species to adequately assess its conservation status.

Discussion

The dorsal colour pattern of *C. mirrityana* sp. nov. consists of blue-grey base colour with a black lateral stripe and bright coloration around the neck and shoulder (Fig. 9A). This strongly resembles the dorsal colour pattern of *C. decresii*, which in association with neighbouring distributions, explains the former classification of the two species as a single taxon. Some populations of *C. fionni* also exhibit markedly similar coloration. For instance, male *C. fionni* from the Lower Eyre Peninsula commonly lack pale dorsal spots, making them difficult to distinguish from *northern C. decresii* (Houston, 1974). Consequently, it is possible that this dorsal colour pattern is an ancestral trait, which has been maintained in *C. mirrityana* sp. nov., *C. decresii*, and some populations of *C. fionni* due to similar selective pressures or through a lack of strong directional selection for alternate coloration.

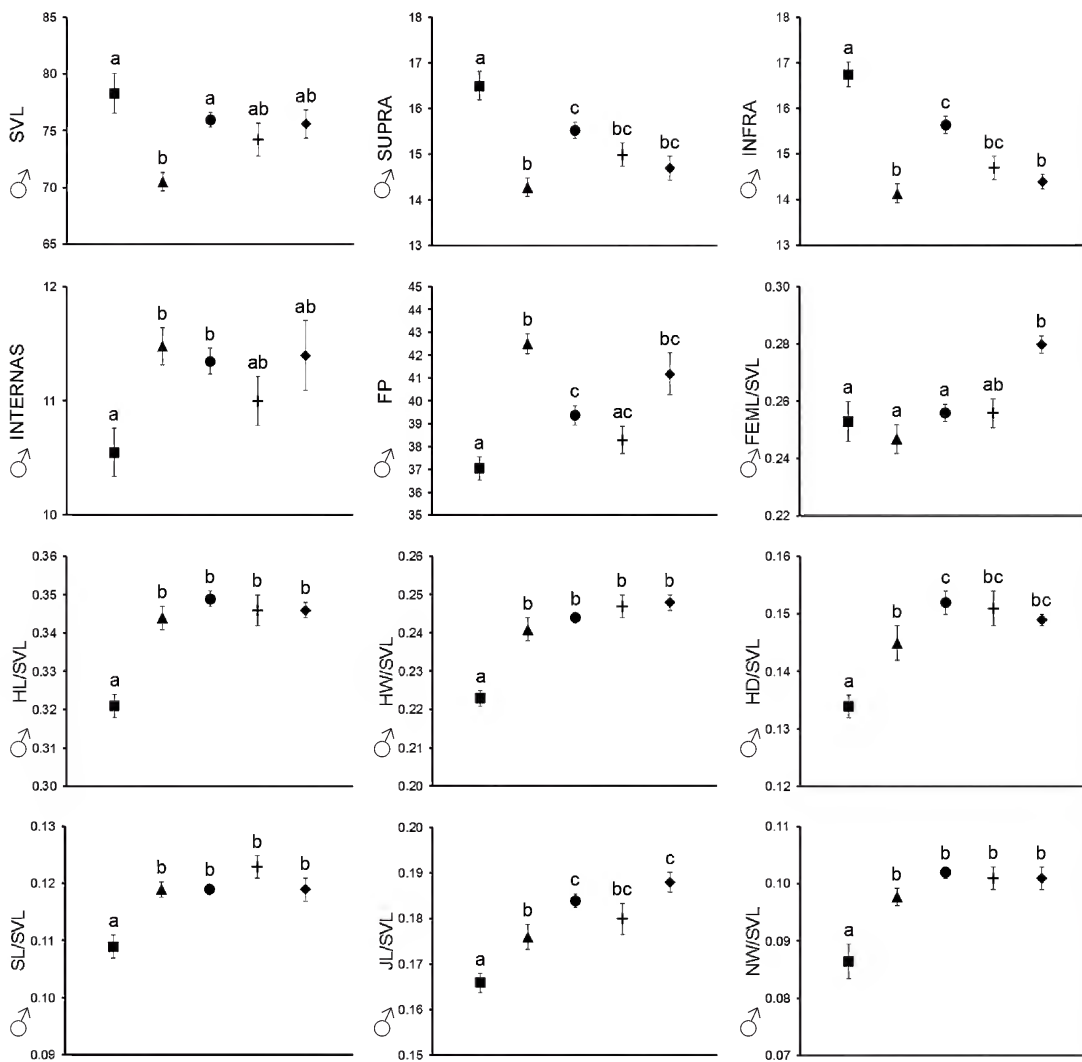


Fig. 5. Comparison between male *Ctenophorus mirrityana* sp. nov. (■), northern *C. decresii* (●), southern *C. decresii* (▲), *C. fionni* (+), and *C. vadhappa* (◆) of measurements and meristic counts showing significant differentiation. Additional characters showing significant pairwise differences were not included as they did not differentiate *Ctenophorus mirrityana* sp. nov. or *C. decresii*. Data are mean \pm standard error.

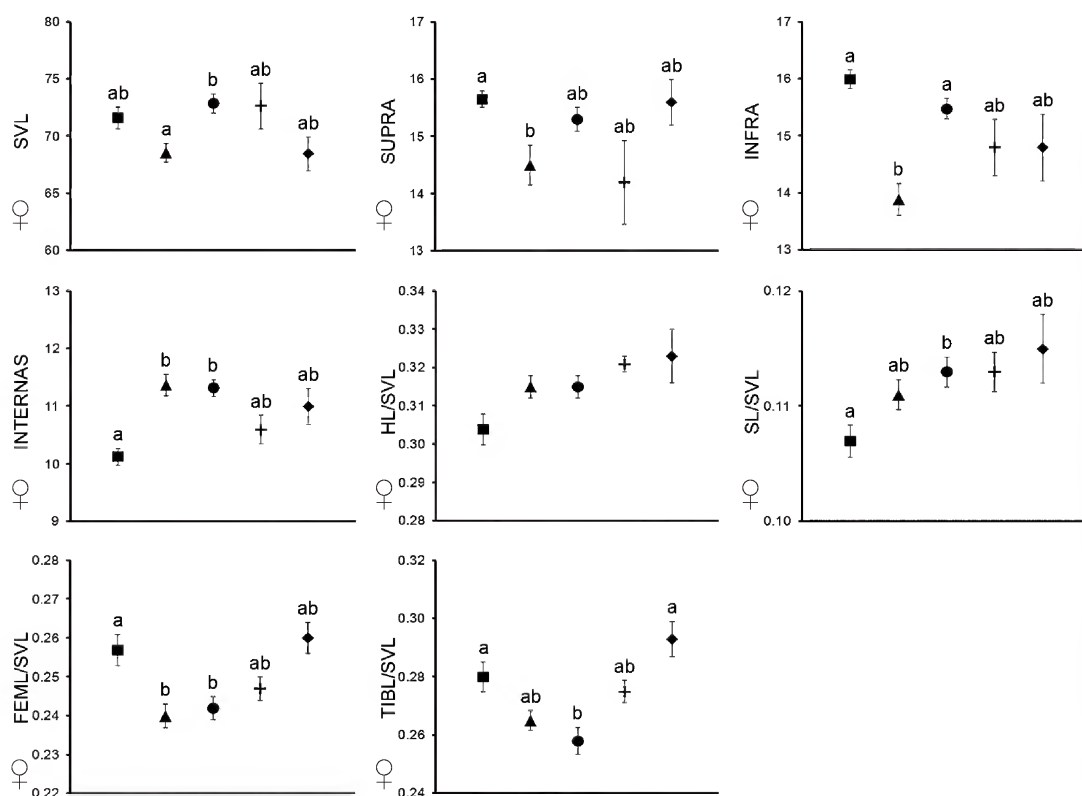


Fig. 6. Comparison between female *Ctenophorus mirrityana* sp. nov. (■), northern *C. decresii* (●), southern *C. decresii* (▲), *C. fionni* (+), and *C. vadhappa* (◆) of measurements and meristic counts showing significant differentiation. Pairwise comparisons of head length (HL/SVL) were not significant. Data are mean \pm standard error.



Fig. 7. Male (A) and female (B) *Ctenophorus mirrityana* sp. nov. from Silverton Wind Farm site, 35 km north west of Broken Hill, NSW (photo S. Sass).

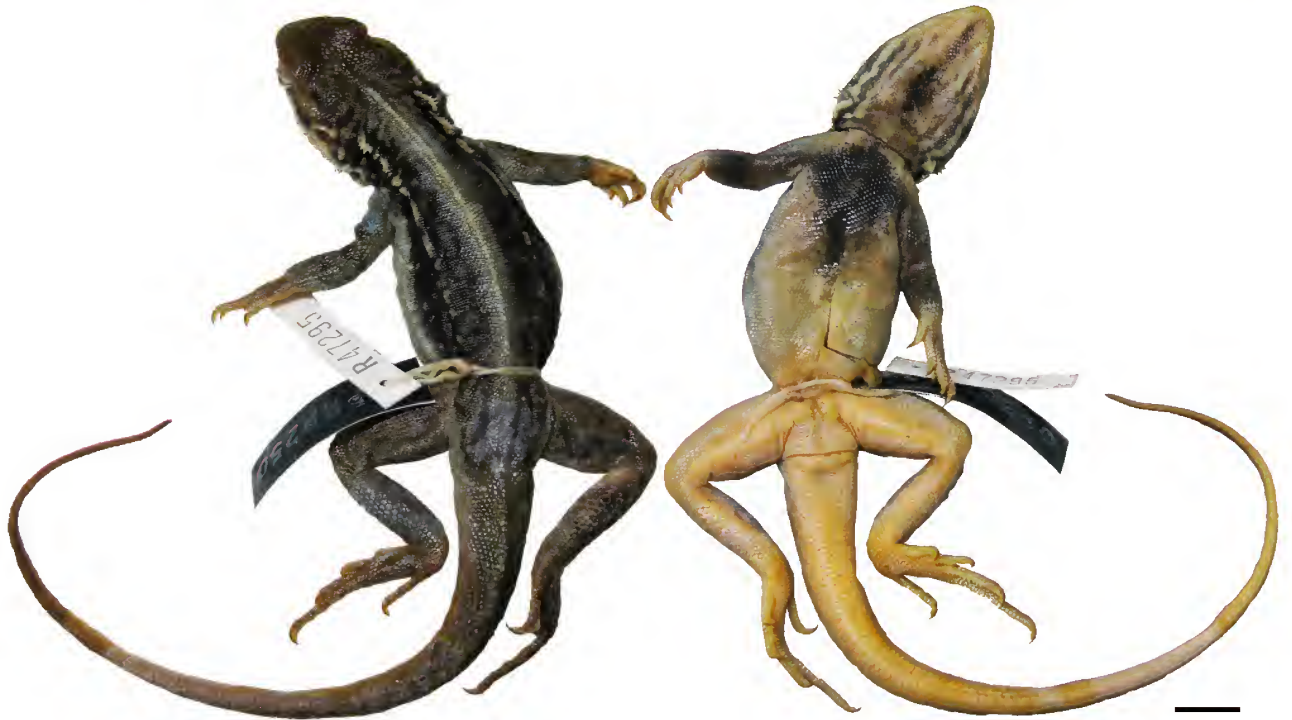


Fig. 8. Holotype of *Ctenophorus mirrityana* sp. nov. (AMS R47295) in dorsal and ventral views. An adult male from Mootwingee National Park, New South Wales. Scale bar = 1 cm.

Coloration and six other morphological characters differentiate *northern* and *southern* *C. decresii* (Fig. 5, 6). These differences are particularly notable given the overall morphological conservatism within the *C. decresii* species complex. For example, we detected little divergence in morphological characters between *northern* *C. decresii* and *C. fionni* males. The current key for *Ctenophorus* distinguishes *C. fionni* from *C. decresii* based on a lack of prominent tubercular scales on the flanks of the former (Houston & Hutchinson, 1998). However, our morphological analysis showed that this is not a reliable distinction as

tubercular scales were not consistently present in *northern* *C. decresii*. A more in-depth comparison of *C. decresii* and *C. fionni* is needed in order to determine reliable defining characters and update the current species key.

In addition to phenotypic differentiation, including throat coloration, there is notable genetic divergence between the *northern* and *southern* lineage of *C. decresii*, with genetic admixture between these lineages geographically restricted, suggesting potential barriers to gene flow (McLean *et al.*, submitted). Taxonomic separation of the *northern* and *southern* lineages is further supported by the lack

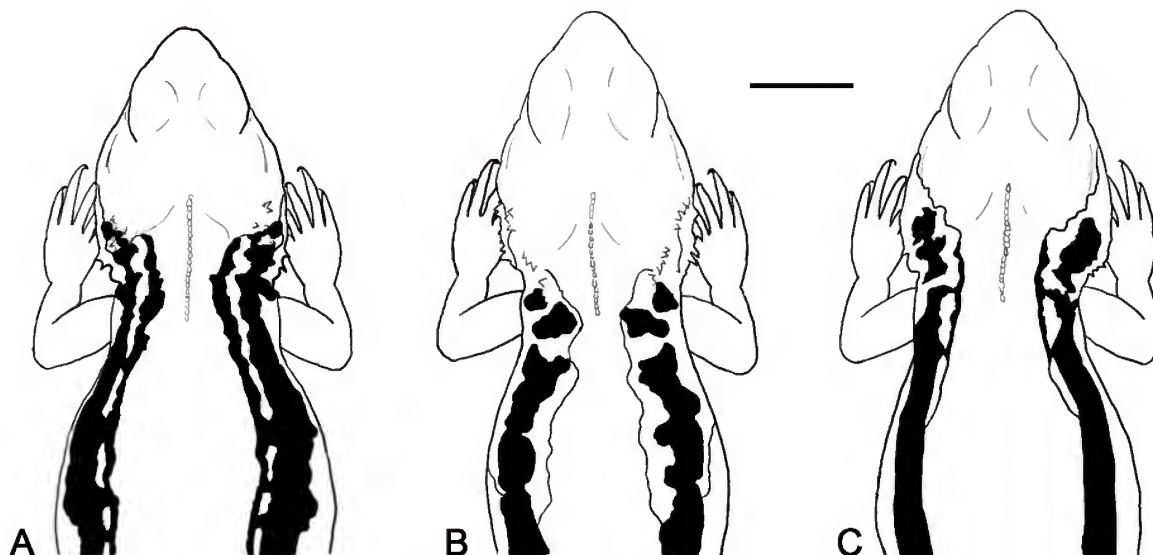


Fig. 9. Dorsal colour pattern, including lateral stripe, and head shape of *Ctenophorus mirrityana* sp. nov. (A), southern *C. decresii* (B), and northern *C. decresii* (C), males. Scale bar = 1 cm.

of phenotypic intermediates detected at the contact zone in the Barossa Valley, SA. Accordingly, we consider the *northern* and *southern* lineages of *C. decresii* as potentially warranting recognition as separate subspecies, with the nominate subspecies *C. decresii decresii* for populations comprising the *southern* lineage, and the *northern* lineage requiring formal description. Future detailed research into the nature of contact between *northern* and *southern C. decresii*, characterising phenotypic, genetic and behavioural variation, is needed to fully resolve the taxonomic status of these lineages.

Species within the *C. decresii* complex are morphologically similar in body form, but divergent in coloration, consistent with a role for coloration in sexual selection and mate recognition. In particular, throat colour appears to be an important signal in this group, likely because this region is displayed during social interactions (Gibbons, 1979; Stuart-Fox & Johnston, 2005). Sexual selection may drive speciation as divergence in mate preference and sexually selected traits (e.g., coloration) may generate reproductive isolation between populations (Panhuis *et al.*, 2001). Consequently, colour divergence among populations appears to be an important component to speciation in the *C. decresii* species complex.

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Appendix 1. Museum material examined.

Southern Ctenophorus decresii

SAM R11358–9, Tea Tree Gully (34°49'S 138°45'E); SAM R12075, Sandy Creek (34°36'S 138°49'E); SAM R13517B, Horsnell Gully National Park (34°56'S 138°43'E); SAM R13968, Black Hill Conservation Park (34°53'S 138°43'E); SAM R23528, Harveys Return, Kangaroo Island (35°45'S 136°38'E); SAM R32772–3, SAM R32777–8, 4 km W Purnong, towards Mannum (34°51'S 139°35'E); SAM R37486, 0.7 km S Snake Lagoon, Kangaroo Island (35°57'36"S 136°39'20"E); SAM R42978, Para River Gorge (34°41'S 138°51'E); SAM R43155, W Trig Point, Black Hill Conservation Park (34°53'S 138°43'E); SAM R45128, Boat Harbour Creek, 1.5 km E Tapanappa Rocks (35°37'56"S 138°16'35"E); SAM R53691, 2.3 km ESE Tapanappa Hill (35°38'01"S 138°16'35"E); SAM R53785, Highland Valley, 7.5 km NNE Strathalbyn (35°11'40"S 138°55'10"E); SAM R54725; SAM R54830, Para Wirra Conservation Park (35°40'10"S 138°49'12"E); SAM R54876, Cudlee Creek Conservation Park (34°50'06"S 138°50'34"E); SAM R54887, Montacute Conservation Park (34°53'15"S 138°47'23"E); SAM R54926, Anstey Hill Recreation Park (34°50'04"S 138°43'55"E); SAM R55041, 2.3 km WNW Blewitt Springs (35°09'36"S 138°34'41"E); SAM R55108–10, Para Wirra Conservation Park (34°43'S 138°48'E); SAM R57376, 0.8 km WNW Monarto Post Office (35°03'14"S 139°06'02"E); SAM R62491, 1.9 km SSW Kanmantoo (35°05'12"S 139°00'16"E); SAM R62501, 2.3 km SSW Kanmantoo (35°05'16"S 138°59'51"E); AMS R81637, AMS R81662–4, AMS R83248, King George Beach, Kangaroo Island (35°39'S 137°07'E); R81638–41, AMS R81665, AMS R83249, Stokes Bay, Kangaroo Island (35°37'S 137°12'E); AMS R92117, Adelaide (34°56'S 138°36'E); N = 40.

Northern Ctenophorus decresii

NMV D13399, 12.8 km S Hawker (31°59'S 138°25'E); NMV D16515, Alligator Gorge (32°45'S 138°03'E); NMV D3411, 3413–4, unknown location; SAM R11357, 20 miles N Peterborough (32°41'S 138°50'E); SAM R12910, Olary Spur (32°17'S 140°20'E); SAM R13797, Oulnina Station, 16 miles SW Manna Hill (32°34'S 139°52'E); SAM R34386, Dare's Ruin near Moorowie reservoir NE Burra (33°17'S 139°04'E); SAM R40690, 2–3, Mallaby Station creekline 6 km WSW sugarloaf hill (33°38'S 139°01'E); SAM R40708, Stone Chimney Creek, 2 km E Burra (33°40'S 138°57'E); SAM R41167, 1 km W Braeuer Homestead (33°11'00"S 139°37'10"E); SAM R41193, 1.8 km SE Tilkilki Homestead (33°05'10"S 139°16'20"E); SAM R41208, 3.5 km E Pandappa (33°10'20"S 139°07'50"E); SAM R41630–1, 2 km E Burra (33°40'30"S 138°57'41"E); SAM R41637–8, 6 km SW Stewarts Old Station (33°07'28"S 139°11'47"E); SAM R44217, Accommodation Hill, 40 km W Blanchtown (34°23'S 139°11'E); SAM R44221, Wilpena Creek (31°31'S 138°39'E); SAM R44452–3, Beetaloo Reservoir (33°11'S 138°12'E); SAM R46292, 3.6 km N Mount Brown (32°28'31"S 138°00'15"E); SAM R51757, 1.77 km S Yudnamutana Bore (30°10'S 139°16'40"E); SAM R51819, 350m WSW Mudlapena Springs (30°36'38"S 138°48'11"E); SAM R51988, 4.1 km N Warden Hill (30°24'23"S 139°13'29"E); SAM R52169, 71, 3.2 km S Partawarta bore, Narrina Station (30°57'30"S 138°43'29"E); SAM R52283, 8 km NNE Willow Springs Homestead (31°23'42"S 138°48'39"E); SAM R52892, 5.7 km SSE Gammon Hill (30°28'06"S 139°02'09"E); SAM R52910, 3.8 km WSW Benbonyathe (30°25'40"S 139°08'42"E); SAM R52935, 7.4 km ESE Mt Serle (30°31'12"S 138°58'26"E); SAM R53001, 4.6 km NE Mt Freeling Height (30°06'39"S 139°24'57"E); SAM R53083–4, 5 km E Mt Elm (31°54'25"S 138°21'36"E); SAM R53106, 3.2 km SSW Dutchmans Peak (32°20'33"S 137°56'31"E); SAM R53112, 1.9 km N Dutchmans Peak (32°18'11"S 137°57'47"E); SAM R53171, 4.5 km NE Callory Bore (31°46'41"S 138°48'11"E); SAM R53217, 1.7 km SW Wilpena Chalet (31°32'35"S 138°35'24"E); SAM R53225, 5 km W Wilpena Chalet (31°31'55"S 138°32'53"E); SAM R53234, 5.5 km WNW Wilpena Chalet (31°30'22"S 138°33'07"E); SAM R53260, 4.5 km ENE Telowie (33°02'31"S 139°07'23"E); SAM R53269, 7.2 km E Telowie (33°03'11"S 138°08'38"E); SAM R57125, Mulga Hill (31°01'00"S 135°38'00"E); SAM R57139–54, unknown location, Flinders Ranges, SAM R58317, 3 km SSW World's End (33°51'48"S 139°02'48"E); SAM R60607, 2.5 km NW Blue Dam (32°04'02"S 140°20'00"E); SAM R60994, 5.5 km NNW Calico Bore (31°58'16"S 140°13'56"E); SAM R62521–2, 4.9 km W Havelock, Chace Range (31°39'55"S 138°40'59"E); SAM R63934, 3.2 km WNW Weeroona Homestead (34°00'26"S 138°57'41"E); SAM R65298, 6.8 km SW Old Manunda Homestead (32°57'11"S 139°43'08"E); SAM R65475, 2.76 km S Tourilie Hill (33°26'29"S 139°06'10"E); N = 70.

Ctenophorus fionni

SAM R12924A, B, Lincoln National Park, Eyre Peninsula (34°55'S 135°55'E); SAM R12929A, B, D, Middleback Range, S Iron Baron (33°03'S 137°09'E); SAM R12930A, Marble Range, Eyre Peninsula (34°27'S 135°30'E); SAM R13054, South Tent Hill, 15 miles WNW Port Augusta (32°24'S 137°31'E); SAM R13323, Euclolo Creek, W Pimba (31°12'S 136°32'E); SAM R13900B, Mt Wedge (33°29'S 135°09'E); SAM R61590, North Neptune Island (35°13'56"S 136°03'51"E); SAM R61596, South Neptune Island (35°19'34"S 136°06'45"E); SAM R61808, North Pearson Island (33°57'40"S 134°16'10"E); SAM R62676, 15.8 km E Hessa Homestead (32°07'54"S 137°34'57"E); SAM R62709, 13.2 km ENE Tallowan Hill (31°26'35"S 130°43'53"E); SAM R66622, 10.1 km NW Cowell (33°36'56"S 136°51'20"E); N = 15.

Ctenophorus vadrappa

SAM R51778, 10.4 km SW Yudnamutana Bore (30°13'20"S 139°11'31"E); SAM R51805, 9 km SSE Mudlapena Springs (30°41'23"S 138°48'57"E); SAM R51870, 2.9 km WNW Mount Fitton (29°58'37"S 139°33'57"E); SAM R51905, 1.8 km NNW Nudlamutana Well (30°21'44"S 139°20'47"E); SAM R51910, 3.2 km SW Stubb's Waterhole (30°19'37"S 139°22'41"E); SAM R51916, 0.5 km NW Nudlamutana Well (30°22'27"S 139°21'02"E); SAM R51970, 7.2 km SW Four Corners Bore (29°54'44"S 138°50'38"E); SAM R52000, 4.2 km NNE Warden Hill (30°24'20"S 139°13'42"E); SAM R52021, 3.8 km S Warden Hill (30°28'35"S 139°12'59"E); SAM R52164 location data unknown; SAM R52213, 0.4 km W Horn Camp Ruin, Alpina Station (31°06'44"S 138°36'56"E); SAM R52321, 7.6 km ESE Molkegna Bore (30°58'31"S 138°50'05"E); SAM R64523, 6.7 km NNE Nantavarrina Homestead (30°49'14"S 138°58'30"E); SAM R65424, 13 km WSW Wertaloona Homestead (30°41'08"S 139°13'01"E); SAM R64632, 5.6 km NNW the John Crossing (30°39'14"S 139°06'47"E); N = 15.

Appendix 2. Comparison of morphological characters, and univariate results for discriminant function analyses based on 24 and 23 variables for males and females respectively. Data are mean \pm standard deviation, with the range of measures indicated in parentheses. All morphometric measures are in mm and sample sizes are listed in the column headings. ANOVA results are presented in the statistics column. Statistically significant values after false discovery rate correction are in bold, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

character	<i>C. mirityana</i> sp. nov. (N = 20♂, 31♀)	southern <i>C. decresii</i> (N = 20♂, 20♀)	northern <i>C. decresii</i> (N = 44♂, 25♀)	<i>C. fionni</i> (N = 10♂, 5♀)	<i>C. vadnappa</i> (N = 10♂, 5♀)	statistics
SVL	78.3 \pm 7.4 (65.0–90.7) 71.6 \pm 5.3 (63.3–84)	70.7 \pm 3.8 (65.2–77.5) 68.5 \pm 3.5 (61.9–74.13)	75.8 \pm 4.4 (66.3–84.6) 72.9 \pm 4.3 (65.1–82.9)	74.2 \pm 4.6 (66.4–83.8) 72.6 \pm 4.5 (68.6–79.6)	75.6 \pm 4.0 (69.1–81.8) 68.5 \pm 3.3 (64.6–72.5)	F_{4,97} = 7.76*** F_{4,80} = 3.15*
AG/SVL	0.40 \pm 0.03 (0.35–0.44) 0.44 \pm 0.04 (0.37–0.53)	0.40 \pm 0.03 (0.32–0.45) 0.44 \pm 0.02 (0.40–0.47)	0.40 \pm 0.03 (0.34–0.46) 0.44 \pm 0.03 (0.37–0.51)	0.38 \pm 0.03 (0.31–0.42) 0.45 \pm 0.02 (0.42–0.47)	0.40 \pm 0.02 (0.37–0.45) 0.45 \pm 0.03 (0.40–0.49)	F _{4,97} = 1.62 F _{4,80} = 0.48
HL/SVL	0.32 \pm 0.01 (0.29–0.36) 0.30 \pm 0.02 (0.28–0.38)	0.34 \pm 0.02 (0.31–0.37) 0.31 \pm 0.01 (0.30–0.35)	0.35 \pm 0.01 (0.33–0.38) 0.32 \pm 0.02 (0.29–0.37)	0.35 \pm 0.01 (0.32–0.37) 0.32 \pm 0.06 (0.31–0.33)	0.35 \pm 0.007 (0.33–0.35) 0.32 \pm 0.02 (0.31–0.35)	F_{4,97} = 13.99*** F_{4,80} = 3.37*
HW/SVL	0.22 \pm 0.008 (0.20–0.24) 0.21 \pm 0.01 (0.20–0.26)	0.24 \pm 0.01 (0.22–0.26) 0.22 \pm 0.008 (0.21–0.24)	0.24 \pm 0.01 (0.22–0.26) 0.22 \pm 0.009 (0.20–0.24)	0.25 \pm 0.009 (0.24–0.26) 0.25 \pm 0.005 (0.21–0.23)	0.25 \pm 0.005 (0.24–0.26) 0.23 \pm 0.01 (0.22–0.24)	F_{4,97} = 17.52*** F _{4,80} = 0.13
HD/SVL	0.13 \pm 0.008 (0.12–0.15) 0.13 \pm 0.009 (0.11–0.16)	0.15 \pm 0.01 (0.13–0.17) 0.13 \pm 0.01 (0.11–0.15)	0.15 \pm 0.01 (0.13–0.18) 0.14 \pm 0.01 (0.12–0.18)	0.15 \pm 0.009 (0.13–0.17) 0.13 \pm 0.01 (0.12–0.15)	0.15 \pm 0.004 (0.14–0.15) 0.14 \pm 0.004 (0.13–0.14)	F_{4,97} = 10.74*** F _{4,80} = 1.59
EYE/SVL	0.07 \pm 0.003 (0.07–0.08) 0.07 \pm 0.006 (0.06–0.09)	0.08 \pm 0.005 (0.06–0.08) 0.07 \pm 0.005 (0.07–0.08)	0.07 \pm 0.006 (0.06–0.09) 0.07 \pm 0.006 (0.06–0.08)	0.08 \pm 0.003 (0.07–0.08) 0.07 \pm 0.003 (0.07–0.08)	0.07 \pm 0.004 (0.07–0.08) 0.08 \pm 0.007 (0.07–0.08)	F _{4,97} = 1.41 F _{4,80} = 0.44
SL/SVL	0.11 \pm 0.008 (0.09–0.12) 0.11 \pm 0.008 (0.10–0.14)	0.12 \pm 0.006 (0.11–0.13) 0.11 \pm 0.006 (0.10–0.12)	0.12 \pm 0.007 (0.10–0.13) 0.11 \pm 0.006 (0.10–0.13)	0.12 \pm 0.006 (0.12–0.13) 0.11 \pm 0.004 (0.11–0.12)	0.12 \pm 0.007 (0.11–0.13) 0.12 \pm 0.007 (0.11–0.13)	F_{4,97} = 10.03*** F_{4,80} = 4.11*
JL/SVL	0.16 \pm 0.009 (0.14–0.19) 0.15 \pm 0.01 (0.13–0.20)	0.18 \pm 0.01 (0.15–0.21) 0.16 \pm 0.009 (0.14–0.17)	0.18 \pm 0.01 (0.16–0.21) 0.16 \pm 0.01 (0.14–0.18)	0.18 \pm 0.01 (0.16–0.19) 0.16 \pm 0.01 (0.15–0.18)	0.19 \pm 0.007 (0.17–0.20) 0.16 \pm 0.009 (0.15–0.17)	F_{4,97} = 11.14*** F _{4,80} = 1.29
NW/SVL	0.09 \pm 0.01 (0.05–0.10) 0.09 \pm 0.008 (0.07–0.11)	0.10 \pm 0.005 (0.09–0.11) 0.10 \pm 0.006 (0.08–0.10)	0.10 \pm 0.007 (0.08–0.12) 0.10 \pm 0.008 (0.07–0.11)	0.10 \pm 0.006 (0.09–0.11) 0.09 \pm 0.007 (0.08–0.10)	0.10 \pm 0.008 (0.09–0.11) 0.09 \pm 0.005 (0.09–0.10)	F_{4,97} = 13.91*** F _{4,80} = 1.36
HUM/SVL	0.15 \pm 0.02 (0.12–0.19) 0.15 \pm 0.02 (0.11–0.19)	0.15 \pm 0.02 (0.12–0.19) 0.15 \pm 0.03 (0.11–0.26)	0.15 \pm 0.02 (0.11–0.19) 0.15 \pm 0.02 (0.11–0.19)	0.16 \pm 0.01 (0.15–0.19) 0.14 \pm 0.02 (0.12–0.16)	0.15 \pm 0.01 (0.13–0.16) 0.16 \pm 0.01 (0.14–0.16)	F _{4,97} = 1.56 F _{4,80} = 0.52
RADL/SVL	0.13 \pm 0.02 (0.11–0.17) 0.14 \pm 0.01 (0.11–0.17)	0.14 \pm 0.009 (0.12–0.15) 0.14 \pm 0.04 (0.11–0.29)	0.14 \pm 0.01 (0.11–0.16) 0.14 \pm 0.01 (0.11–0.16)	0.13 \pm 0.01 (0.11–0.15) 0.13 \pm 0.01 (0.12–0.15)	0.15 \pm 0.01 (0.13–0.16) 0.15 \pm 0.007 (0.14–0.16)	F _{4,97} = 2.68 F _{4,80} = 0.63
HAND/SVL	0.17 \pm 0.02 (0.14–0.22) 0.19 \pm 0.02 (0.15–0.22)	0.18 \pm 0.01 (0.16–0.21) 0.18 \pm 0.01 (0.15–0.20)	0.17 \pm 0.02 (0.12–0.21) 0.18 \pm 0.02 (0.14–0.21)	0.17 \pm 0.02 (0.14–0.21) 0.17 \pm 0.008 (0.16–0.18)	0.18 \pm 0.02 (0.15–0.20) 0.18 \pm 0.02 (0.15–0.20)	F _{4,97} = 0.51 F _{4,80} = 1.08
FING/SVL	0.10 \pm 0.01 (0.08–0.13) 0.12 \pm 0.01 (0.10–0.14)	0.11 \pm 0.01 (0.09–0.14) 0.11 \pm 0.01 (0.08–0.13)	0.10 \pm 0.01 (0.08–0.14) 0.11 \pm 0.01 (0.07–0.13)	0.10 \pm 0.01 (0.09–0.12) 0.10 \pm 0.008 (0.09–0.11)	0.10 \pm 0.01 (0.08–0.12) 0.11 \pm 0.01 (0.10–0.13)	F _{4,97} = 0.30 F _{4,80} = 1.45
FEML/SVL	0.25 \pm 0.03 (0.20–0.32) 0.26 \pm 0.02 (0.21–0.30)	0.25 \pm 0.02 (0.21–0.29) 0.24 \pm 0.01 (0.21–0.26)	0.26 \pm 0.02 (0.21–0.29) 0.24 \pm 0.02 (0.21–0.28)	0.26 \pm 0.01 (0.24–0.28) 0.25 \pm 0.007 (0.25–0.27)	0.28 \pm 0.01 (0.26–0.29) 0.26 \pm 0.008 (0.25–0.27)	F_{4,97} = 4.37** F_{4,80} = 4.12*
TIBL/SVL	0.27 \pm 0.03 (0.21–0.33) 0.28 \pm 0.03 (0.22–0.34)	0.27 \pm 0.02 (0.23–0.31) 0.27 \pm 0.01 (0.23–0.30)	0.27 \pm 0.02 (0.22–0.32) 0.26 \pm 0.02 (0.22–0.31)	0.29 \pm 0.01 (0.28–0.32) 0.28 \pm 0.008 (0.27–0.29)	0.31 \pm 0.01 (0.29–0.33) 0.29 \pm 0.01 (0.28–0.31)	F_{4,97} = 6.99*** F_{4,80} = 4.76*
FOOT/SVL	0.36 \pm 0.04 (0.30–0.44) 0.35 \pm 0.03 (0.30–0.41)	0.37 \pm 0.02 (0.33–0.42) 0.35 \pm 0.03 (0.30–0.41)	0.35 \pm 0.03 (0.30–0.42) 0.34 \pm 0.02 (0.28–0.40)	0.36 \pm 0.02 (0.34–0.40) 0.34 \pm 0.02 (0.32–0.36)	0.39 \pm 0.008 (0.38–0.40) 0.36 \pm 0.02 (0.34–0.39)	F_{4,97} = 4.58** F _{4,80} = 1.59
TOE/SVL	0.20 \pm 0.02 (0.16–0.24) 0.20 \pm 0.01 (0.17–0.23)	0.21 \pm 0.02 (0.17–0.26) 0.19 \pm 0.02 (0.16–0.24)	0.20 \pm 0.02 (0.15–0.25) 0.19 \pm 0.02 (0.14–0.22)	0.20 \pm 0.01 (0.18–0.22) 0.19 \pm 0.01 (0.17–0.20)	0.22 \pm 0.01 (0.20–0.23) 0.20 \pm 0.03 (0.18–0.24)	F_{4,97} = 3.42* F _{4,80} = 1.88
SUPRA	16.5 \pm 1.3 (14–19) 15.7 \pm 0.8 (14–17)	14.3 \pm 0.9 (12–16) 14.5 \pm 1.5 (12–18)	15.5 \pm 1.2 (13–18) 15.3 \pm 1.0 (13–17)	15 \pm 0.8 (14–16) 14.2 \pm 1.6 (12–16)	14.7 \pm 0.8 (14–16) 15.6 \pm 0.9 (15–17)	F_{4,97} = 9.48*** F_{4,80} = 4.50*
INFRA	16.7 \pm 1.1 (15–19) 16 \pm 0.9 (15–18)	14.1 \pm 0.09 (12–15) 13.9 \pm 1.2 (11–16)	15.7 \pm 1.2 (13–18) 15.5 \pm 0.9 (14–18)	14.7 \pm 0.8 (13–16) 14.8 \pm 1.1 (14–16)	14.4 \pm 0.5 (14–15) 14.8 \pm 1.3 (13–16)	F_{4,97} = 17.27*** F_{4,80} = 13.64**
ROSNAS	4.8 \pm 0.8 (4–6) 4.8 \pm 0.6 (4–6)	4.6 \pm 0.5 (4–5) 4.5 \pm 0.6 (4–6)	4.7 \pm 0.5 (4–6) 4.5 \pm 0.5 (4–5)	4.4 \pm 0.5 (4–5) 4.4 \pm 0.5 (4–5)	4.5 \pm 0.5 (4–5) 5 \pm 0.7 (4–6)	F _{4,97} = 0.93 F _{4,80} = 2.31
SUPRANAS	5.1 \pm 0.7 (4–7) 4.9 \pm 0.4 (4–6)	4.95 \pm 0.4 (4–6) 5 \pm 0.5 (4–6)	5.3 \pm 0.6 (4–6) 4.9 \pm 0.5 (4–6)	5.1 \pm 0.7 (4–6) 5.6 \pm 0.9 (5–7)	5.1 \pm 0.6 (4–6) 5.2 \pm 0.4 (5–6)	F _{4,97} = 0.71 F _{4,80} = 2.63
INTERNAS	10.6 \pm 0.9 (9–12) 10.1 \pm 0.8 (9–12)	11.4 \pm 0.7 (10–13) 11.4 \pm 0.8 (10–13)	11.4 \pm 0.8 (10–13) 11.3 \pm 0.9 (9–13)	11 \pm 0.7 (10–12) 10.6 \pm 0.5 (10–11)	11.4 \pm 1.0 (10–13) 11 \pm 0.7 (10–12)	F_{4,97} = 5.51** F_{4,80} = 9.95**
SDL	23.7 \pm 1.7 (21–27) 23.7 \pm 1.6 (21–27)	25.4 \pm 1.6 (23–29) 24.1 \pm 1.9 (21–27)	24.5 \pm 1.7 (19–27) 24.5 \pm 1.6 (21–27)	23.8 \pm 1.2 (22–26) 23.8 \pm 1.8 (22–26)	24.7 \pm 0.6 (23–27) 25.2 \pm 0.8 (24–26)	F_{4,97} = 3.51* F _{4,80} = 1.44
FP	37.1 \pm 2.1 (34–42)	42.4 \pm 2.0 (40–46)	39.5 \pm 2.8 (34–45)	38.3 \pm 1.9 (36–42)	41.2 \pm 2.9 (36–45)	F_{4,97} = 14.04***

Appendix 3. Pearson correlation coefficients between male morphological characters.

	SVL	SUPRA	INFRA	ROSNAS	SUPRANAS	INTERNAS	SDL	FP	HL_SVL	HW_SVL	HD_SVL	FEML_SVL	TIBL_SVL	FOOT_SVL	TOE_SVL	AG_SVL	EYE_SVL	SL_SVL	JL_SVL	NW_SVL	HUML_SVL	RADL_SVL	HAND_SVL	FING_SVL
SVL	.																							
SUPRA	0.31	.																						
INFRA	0.29	0.76	.																					
ROSNAS	-0.38	0.37	0.29	.																				
SUPRANAS	0.20	0.26	0.32	0.22	.																			
INTERNAS	-0.06	0.05	0.03	0.08	0.33	.																		
SDL	-0.06	-0.16	-0.11	0.10	0.18	0.26	.																	
FP	-0.17	-0.25	-0.29	-0.18	-0.04	0.32	0.21	.																
HL_SVL	-0.22	-0.11	-0.18	-0.03	0.12	0.22	0.06	0.10	.															
HW_SVL	-0.29	-0.17	-0.26	-0.06	0.01	0.30	0.06	0.18	0.78	.														
HD_SVL	-0.01	-0.26	-0.27	-0.19	-0.15	-0.02	0.01	0.07	0.47	0.48	.													
FEML_SVL	-0.31	-0.07	-0.11	0.04	-0.12	-0.07	0.03	-0.02	0.07	0.13	0.12	.												
TIBL_SVL	-0.30	-0.24	-0.32	0.00	-0.18	-0.13	-0.08	-0.05	0.11	0.14	0.18	0.67	.											
FOOT_SVL	-0.53	-0.21	-0.27	0.14	0.02	-0.07	0.13	0.15	0.00	0.09	0.01	0.63	0.67	.										
TOE_SVL	-0.49	-0.11	-0.18	0.20	0.02	0.06	0.14	0.24	0.09	0.08	0.00	0.57	0.53	0.84	.									
AG_SVL	0.21	0.02	0.10	-0.08	-0.07	0.03	0.09	0.16	-0.16	-0.17	0.03	-0.08	-0.20	-0.17	-0.15	.								
EYE_SVL	-0.37	-0.22	-0.12	-0.01	-0.02	-0.07	-0.03	-0.06	0.31	0.22	0.12	0.16	0.04	0.10	0.14	-0.13	.							
SL_SVL	-0.27	-0.22	-0.30	-0.02	0.08	0.22	0.07	0.05	0.65	0.59	0.35	0.06	0.19	0.14	0.13	-0.26	0.16	.						
JL_SVL	-0.07	-0.09	-0.10	-0.23	0.04	0.21	-0.02	0.17	0.66	0.64	0.41	0.02	0.00	-0.16	-0.11	-0.13	0.13	0.34	.					
NW_SVL	-0.05	-0.21	-0.31	-0.08	-0.09	0.13	0.05	0.16	0.52	0.52	0.50	0.11	0.26	0.06	0.11	0.05	0.11	0.50	0.41	.				
HUML_SVL	-0.36	-0.04	-0.09	-0.10	-0.08	-0.06	-0.13	-0.01	0.15	0.09	0.07	0.37	0.35	0.28	0.27	-0.24	0.16	0.17	0.13	0.10	.			
RADL_SVL	-0.29	0.01	-0.05	0.11	0.21	-0.01	0.21	0.01	0.21	0.20	0.06	0.55	0.45	0.42	0.41	0.08	0.02	0.17	0.12	0.27	0.33	.		
HAND_SVL	-0.51	-0.09	-0.17	0.05	-0.03	-0.06	0.05	0.07	0.15	0.18	0.03	0.52	0.40	0.63	0.62	-0.20	0.20	0.19	-0.04	0.16	0.34	0.44	.	
FING_SVL	-0.45	-0.05	-0.13	-0.02	0.07	-0.02	0.12	0.00	0.12	0.11	0.04	0.45	0.35	0.58	0.53	-0.09	0.27	0.11	-0.02	0.13	0.26	0.31	0.75	.

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